第34卷 第4期 古脊椎动物学报 pp. 253—268
1996年 10月 VERTEBRATA PALASIATICA figs. 1—4, pl. I

大瓣鱼科一新属与历史动物地理学研究

朱 敏 王俊卿
(中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要 描述了采自云南曲靖龙华山下泥盆统徐家冲组顶部的一件大瓣鱼科化石，定名为龙华全瓣鱼(*Holopetalichthys longhuaensis* gen. et sp. nov.)。对新属种与其它瓣甲鱼类的比较表明全瓣鱼是最原始的大瓣鱼类，它与其余的大瓣鱼类构成姊妹群。通过对大瓣鱼科的历史动物地理学研究认为，瓣甲鱼目起源于华南，而大瓣鱼科的祖先几乎是广布的。大瓣鱼科隔离分化模式显示，在泥盆纪期间，华南区与东冈瓦纳区有较密切的联系

关键词 云南曲靖，下泥盆统，大瓣鱼科，历史动物地理学
中图法分类号 Q915.862, Q915.1

一、引 言

大瓣鱼科(Macropetalichthyidae)化石的最初发现限于北美与欧洲(Norwood & Owen, 1846; Stensiö, 1925; Broili, 1929)。Woodward(1941)根据澳大利亚材料建立的椎瓣鱼属(*Notopetalichthys*)代表了大瓣鱼科在欧美大陆之外的首次发现。我国大瓣鱼科化石的研究始于潘江等(1975)，他们建立了中华瓣甲鱼属(*Sinopetalichthys*)。其后，在澳大利亚和华南又发现了许多大瓣鱼类材料(Young, 1978, 1985; 潘江、王士涛，1978; 刘时藩，1981; 王士涛、曹仁关，1988)，既有广布性属种(如 *Lunaspis*, *Wijdeaspis*)，又有地区性属种(如 *Sinopetalichthys*, *Shearsbyaspis*)，这表明澳大利亚和华南是重要的大瓣鱼科地理分布区。与大瓣鱼科同属瓣甲鱼目的还有拟瓣鱼科(Quasipetalichthyidae, 刘玉海，1973; 潘江等，1987; Liu, 1991) 和滇东瓣甲鱼属(*Diandongpetalichthys*, 潘江、王士涛，1978; Zhu, 1991)，后两者具较多的原始特征，并且仅仅分布于华南与宁夏的中古生代地层中。因此，华南早期大瓣鱼类的发现与研究将有助于探讨大瓣鱼科的起源与演化。

本文描述的一件大瓣鱼类化石采自云南曲靖市龙华山下泥盆统徐家冲组顶部的紫红色细砂岩中。在该层位之下曾发现云南鱼类(Zhu, in press)和总鳍鱼类碎片，而紧接其上是穿洞组(或广义的海口组)的底砾岩。在曲靖西山区徐家冲附近，该组中发现的早期脊椎动物化石还有盔甲鱼类 *Eugaleaspis xujiachongensis*(刘玉海，1975), *Sanchaspis magalarostrata*(潘江、王士涛，1981), *Pterogonaspis yuhaii*(朱敏，1992), *Gantarostraspis geni*(朱敏等，1994)和节甲鱼类 *Szelepis yunnanensis*(刘玉海，1979; 方润森等，1985)，伴生植物化石有 *Zosterophyllum yunnanicum*, *Drepanophycus spinaeformis* 等(方润森等，1985)，

收稿日期：1995-05-15

含鱼层位与龙华山的层位相比要略低些。关于徐家冲组的时代，朱敏等(1994)已作详细讨论，认为是晚 Pragian 期至早 Emsian 期。

二、系 统 描 述

盾皮鱼亚纲 Placodermi M'Coy，1848

瓣甲鱼目 Petalichthyida Jaekel，1911

大瓣鱼科 Macropetalichthyidae Eastman，1898

全瓣鱼属(新属) *Holopetalichthys* gen. nov.

属型种　龙华全瓣鱼(新属、新种) *Holopetalichthys longhuaensis* gen. et sp. nov.

属征　个体很小的大瓣鱼类。吻片与松果片接触，完全分隔两侧的眶前片。后凹线沟向中线后伸，颈片骨化中心位于骨片后半部。眶上感觉管未与后凹线沟辏合。

属名由来　*Holo*-(Gr.)"全"; *petalichthys*(Gr.) 意为"瓣鱼"，瓣甲鱼类化石属名多引用该词干与词根。整个属名意指该鱼已是典型的大瓣鱼类，而有别于拟瓣鱼类和滇东瓣甲鱼。

龙华全瓣鱼(新属、新种) *Holopetalichthys longhuaensis* gen. et sp. nov.

(图1；图版Ⅰ)

种征　同属征。

正型标本　一件完整的颅顶甲标本(中国科学院古脊椎动物与古人类研究所编号：V9765)。

种名由来　取自标本产地云南曲靖市龙华山。

产地与层位　云南曲靖市龙华山，徐家冲组顶部，早泥盆世早 Emsian 期。

描述　标本存在一定程度的变形。尤其是颅顶甲左后侧向下折曲，只能侧视。此外，膜质骨受到不同程度的磨蚀，但也因此能够了解骨骼内面的一些构造，譬如松果坑、感觉管系统。

颅顶甲中长3.7cm，最大宽度2.9cm。长宽比为1.28。在已知的大瓣鱼类中，颅顶甲最长可达到25cm，如 *Macropetalichthys rapheidolabis* (Denison，1978)，小的如 *Ellopetalichthys* (Ørvig，1957)，*Shearsbyaspis* (Young，1985) 也有5cm左右长。可以看出，龙华山标本是目前大瓣鱼类中最小的颅顶甲，与滇东瓣甲鱼(Zhu，1991)相仿。

在大瓣鱼类中，从颅顶甲的整体形态看，新属与 *Shearsbyaspis* (Young，1985)，*Lunaspis* (Gross，1961)，*Notopetalichthys* (Ørvig，1957) 较接近。颅顶甲的前缘突出，侧缘向后在眶孔的前侧方有一内凹，最宽处位于关节缘前突之间，关节缘(om，图1)朝向侧后方。与 *Lunaspis* 凸出的后缘不同，新属后缘稍内凹。*Shearsbyaspis* 和 *Notopetalichthys* 颅顶甲后缘没有保存。

眶孔(orb，图1)保存较好，为颅顶甲所封闭。这是大瓣鱼科的一条重要离征。新属眶孔相对较大，长约6mm，占颅顶甲总长的16%。在两眶孔之间，清晰可见松果坑

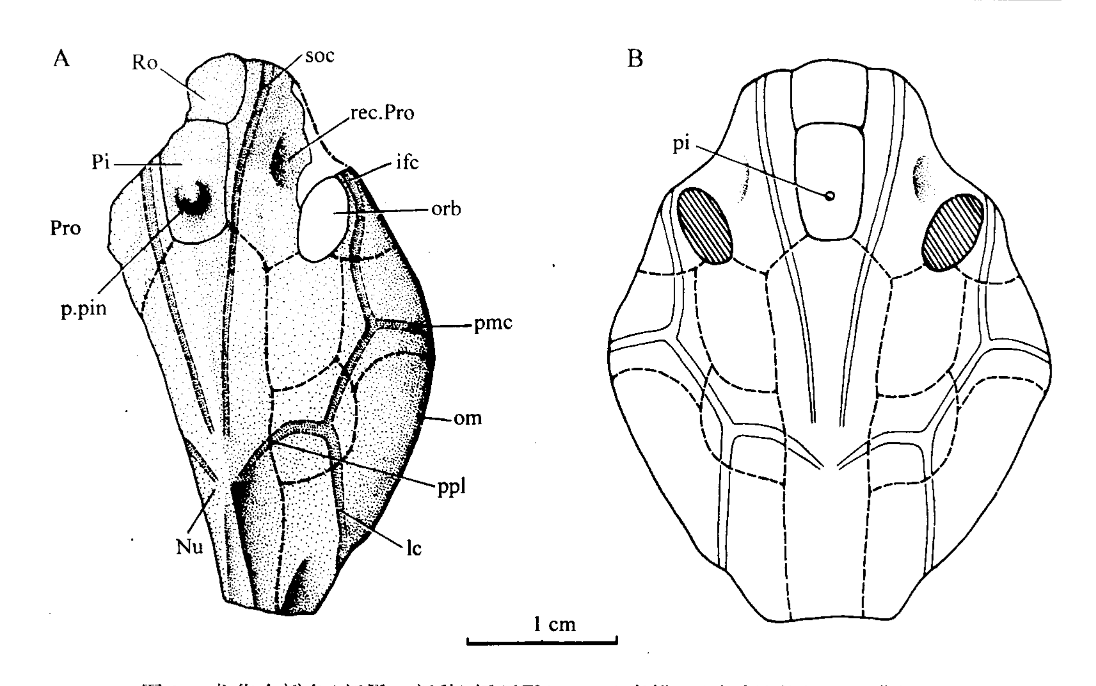


图1　龙华全瓣鱼(新属、新种)颅顶甲(V9765)素描(A)与复原图(B)，背视

Fig. 1　The sketch (A) and reconstruction (B) of the skull roof of *Holopetalichthys longhuaensis* gen. et sp. nov. (V9765) in dorsal view

ifc，眶下感觉管 infraorbital sensory canal；lc，主侧线管 main lateral line canal；Nu，颈片 nuchal plate；om，关节缘 obstantic margin；orb，眶孔 orbital opening；Pi，松果片 pineal plate；pi，松果孔 pineal opening；pmc，后缘感觉管 postmarginal sensory canal；p.pin，松果坑 pineal pit；ppl，后凹线沟 posterior pitline；Pro，眶前片 preorbital plate；rec. Pro，眶前凹 preorbital recess；Ro，吻片 rostral plate；soc，眶上感觉管 supraorbital sensory canal

(p. pin，图1)的内模(此处膜质骨基本被磨蚀掉)。松果坑较大，相对于眶孔的位置在大瓣鱼科中与 *Shearsbyaspis*、*Lunaspis* 等相同。沿中轴线，颅顶甲在松果坑之前比较明显地向下延伸，在最后部有一个很窄的倒V形的凹陷。此外，在眶孔的紧前方颅顶甲有一个小的凹陷，类似的凹陷被认为普遍见于大瓣鱼科中，如 *Shearsbyaspis* (Young, 1985)。

颅顶甲的骨缝界线很不清楚，可以辨认的是吻片(Ro，图1)与松果片(Pi，图1)。其余骨片只能依据感觉管系统作大致恢复。吻片与松果片接触，隔开两侧的眶前片。这种类型的吻片与松果片的关系在大瓣鱼科中还见于 *Shearsbyaspis* (Young, 1985)。吻片相对较短，前缘突出。松果片呈长方形，腹面有松果坑。在松果片之后，构成颅顶甲中列的应是很长的颈片(Nu，图1)。颅顶甲的纹饰为瘤点，没有形成细脊。

感觉管系统保存得相当好，为典型的瓣甲鱼型(Zhu, 1991)。在瓣甲鱼类中，眶上感觉管和后凹线沟向颈片的骨化中心延伸，它们或者辏合在一起，如 *Macropetalichthys*、*Sinopetalichthys*，或者仍相互分开，如 *Lunaspis*。新属的后凹线沟(ppl，图1)向中线后

伸，颈片骨化中心位于骨片后半部，这同已知大瓣鱼类构成明显对比。在其它大瓣鱼类中，后凹线沟向中线平伸或前伸，颈片骨化中心位于骨片前半部。此外，新属眶上感觉管(soc，图 1)和后凹线沟没有辏合在一起，类似 *Lunaspis*。

三、比较与讨论

1. 与滇东瓣甲鱼和新瓣鱼的比较

本文第一作者对以滇东瓣甲鱼为代表的一类瓣甲鱼类化石作了深入的形态学研究，并建立了瓣甲鱼目的一个新科天池鱼科(Tianchiidae)[1]。它们与全瓣鱼的相似处包括后凹线沟向中央后伸，颈片骨化中心位于骨片后半部。不同之处主要在于全瓣鱼的颅顶甲已形成封闭的眶孔，这是大瓣鱼科的一条重要离征。

2. 与拟瓣鱼和宽甲鱼的比较

相似点包括它们的颅顶甲都已丢失后鼻片，吻片与松果片完全分隔两侧的眶前片。不同点在于拟瓣鱼和宽甲鱼的眶孔仍然是侧位的(Liu，1991)，而全瓣鱼的眶孔已被颅顶甲所封闭。

3. 与大瓣鱼科现有属的比较

在大瓣鱼科的现有属中，全瓣鱼与 *Shearsbyaspis* (Young，1985)最接近，它们既没有象 *Macropetalichthys*，*Xinanpetalichthys*，*Wijdeaspis* 等那样，吻片与松果片愈合成一块骨片，也没有象 *Lunaspis*，*Notopetalichthys*，*Sinopetalichthys* 那样，吻片与松果片为眶前片所分开。但根据外类群比较，全瓣鱼与 *Shearsbyaspis* 之间的相似处(吻片与松果片接触，完全分隔两侧的眶前片)属于大瓣鱼科的祖征。该特征同样见于拟瓣鱼科(Liu，1991)。全瓣鱼与 *Shearsbyaspis* 之间的区别主要有两点。首先，全瓣鱼的纹饰仍为瘤点状，而 *Shearsbyaspis* 的纹饰已象 *Lunaspis*，*Sinopetalichthys* 那样形成网状低脊，呈较规则的同心圆或放射状排列。其次，全瓣鱼的后凹线沟向中线后伸，颈片骨化中心位于骨片后半部，而 *Shearsbyaspis* 的后凹线沟向中线前伸，颈片骨化中心位于骨片前半部。

4. 全瓣鱼系统位置的初步研究

加上本文描述的新属，大瓣鱼科已有十个属，它们与拟瓣鱼科，滇东瓣甲鱼以及新瓣鱼共同隶属瓣甲鱼亚目。然而，对于大瓣鱼科这些属之间相互关系的讨论，迄今为止仍然停留在比较的阶段，尚未进行系统演化方面的研究，这部分是由于化石材料的限制。实际上，通过建立分支图的方法来讨论大瓣鱼科内类群系统发育关系是可行的。按照分支系统学的哲学基础，所有的分支图都是能够被检验的假说。通过对这些假说的不断证实或证伪，分支图就可能愈来愈真实地恢复生物本来的演化历史。换句话说，分支

---

1) 朱敏，1990：云南曲靖晚志留世—早泥盆世瓣甲鱼类的系统研究(博士学位论文)。

图的建立提供了今后讨论的基础或框架。

由于在大瓣鱼科中能够被用来建立分支图的离征相当有限，本文所提出的分支图(图2)仅是一个初步结果。颅顶甲已形成封闭的眶孔，这是定义大瓣鱼科的最重要的一条离征(Zhu，1991)。另一条可能的离征是颅顶甲的眶前凹陷，见于 *Shearsbyaspis*，*Lunaspis*，*Wijdeaspis*(Young，1985) 以及全瓣鱼等。在性状分析中，拟瓣鱼科和滇东瓣甲鱼作为大瓣鱼科的外类群，用于判定大瓣鱼科的性状极向。在大瓣鱼科中，全瓣鱼颅顶甲后凹线沟向中线后伸，颈片骨化中心位于骨片后半部，该特征在以滇东瓣甲鱼为代表的一类瓣甲鱼中也可以见到，其生长系列研究表明后凹线沟向中线后伸应为祖征。根据外类群比较，吻片与松果片接触，并完全分隔两侧的眶前片对于大瓣鱼科而言也是祖

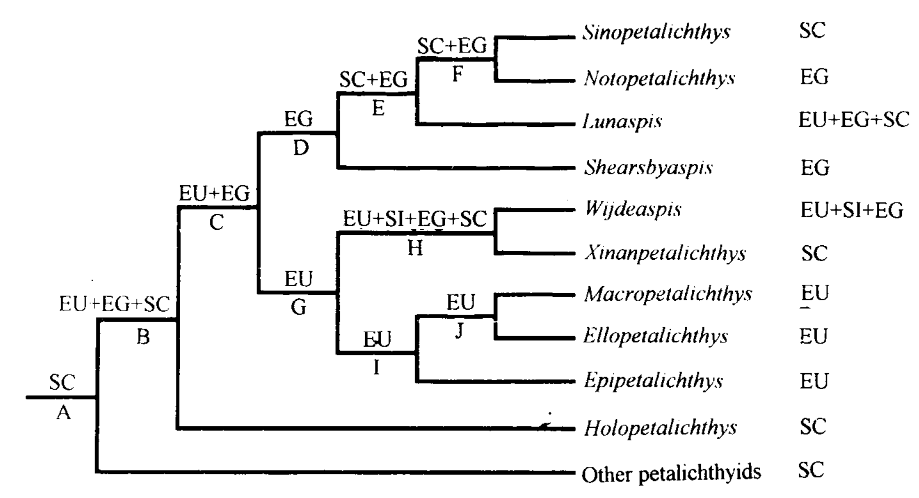


图2 大瓣鱼科的支序图，以及大瓣鱼和瓣甲鱼类的祖先分布(依据系统发育生物地理学)
离征：结点A(瓣甲鱼目)—瓣甲鱼型感觉管系统，纵长形关节凹；B(大瓣鱼科)—颅顶甲形成封闭的眶孔；C—后凹线沟向中线平伸或前伸，颈片骨化中心位于骨片前半部；D—脊纹(在 *Notopetalichthys* 中性状逆转)；E—吻片与松果片分离，两侧眶前片在中央接触；F—眶孔较远离颅顶甲边缘，眶后片眶下部较宽；G—吻片与松果片愈合；H—吻—松果片前缘后凹；I—颅顶甲关节缘朝向侧面；J—眶上感觉管与后凹线沟矮合(在 *Sinopetalichthys* 中平行进化)

Fig. 2 The cladogram of the Macropetalichthyidae, and phylogenetic biogeographic (Hennigian dispersal) analyses of ancestral distribution of macropetalichthyids and petalichthyids
Synapomorphies: Node A (Petalichthyida) — petalichthyid pattern of sensory canal system, longitudinal glenoid fossa; Node B (Macropetalichthyidae) — enclosed orbits in skull roof; Node C—posterior pitline projecting horizontally or anteriorly, ossification center of nuchal plate in anterior half of the plate; Node D—dermal bones ornamented with ridges (reversal in *Notopetalichthys*); Node E—rostral and pineal plates separated, preorbital plates of both sides contacting in midline; Node F—orbital opening relatively far away from the margin of skull roof, suborbital portion of postorbital plate fairly broad; Node G—rostral and pineal plates fused into a rostropineal plate; Node H—anterior margin of rostro-pineal plate concave; Node I—obstantic margin of skull roof facing laterally; Node J—supraorbital sensory canals and posterior pit-lines confluent (parallelism in *Sinopetalichthys*)

征。因此，笔者认为全瓣鱼是最原始的大瓣鱼类，与其余大瓣鱼类构成姊妹群。后者颅顶甲后凹线沟向中线平伸或前伸，颈片骨化中心位于骨片前半部。

除全瓣鱼之外的大瓣鱼类可进一步分成两大分支，代表两个演化方向。第一大分支以 *Shearsbyaspis*, *Lunaspis* 为代表，其膜质骨的纹饰为网状低脊，并呈规则排列。*Notopetalichthys* 虽然没有该类脊纹，但它的吻片与松果片分离，两侧眶前片在中央接触，眶孔较远离颅顶甲边缘等特征与 *Sinopetalichthys* 相近，因此，根据简约性原理，将 *Notopetalichthys* 作为 *Sinopetalichthys* 的姊妹群(图 2)。另一大分支以 *Macropetalichthys*, *Wijdeaspis* 为代表，它们的吻片与松果片已愈合成一块骨片。

四、大瓣鱼科的历史动物地理学

1. 中古生代脊椎动物地理区系

Young (1981) 结合地质与地球物理证据，提出了早泥盆世期间五大脊椎动物地理区系，它们是欧美区(头甲类区)，东冈瓦纳区(乌塔古纳鱼类－叶鳞鱼类区)，华南区(盔甲类－云南鱼类区，包括越南北部)，西伯利亚区(双甲类区)和图瓦区(塔努鱼类区)。其中，图瓦区是一个较小的脊椎动物地理区系，在大多数泥盆纪古地理复原图上，图瓦盆地是作为西伯利亚板块的一部分(Young, 1990, 1993)。欧美区又被称为"老红大陆"，包括劳伦斯区，波罗的海区和阿摩里卡区(Young, 1986)。因此，讨论中古生代早期脊椎动物地理分布，最基本的问题是前四个大区系的关系。

除上述五个区系外，在中古生代期间，具脊椎动物化石的古地理单元还有哈萨克斯坦区，西冈瓦纳区和塔里木。另有一些单元，如土耳其、伊朗、阿拉伯古陆，掸一泰地块(包括我国滇西)，在此期间贴在冈瓦纳大陆的北缘。哈萨克斯坦区主要产胴甲鱼类化石，其地方性的属如 *Tenizolepis*, *Stegolepis* (Malinovskaya, 1973, 1989) 与华南泥盆系地层中的湖南鱼(*Hunanolepis*)、江西鱼(*Jiangxilepis*)有很近的亲缘关系(Young, 1993; Zhu, in press)，指示这两个古动物地理区之间的联系。西冈瓦纳区处于欧美区与东冈瓦纳区之间，在动物群面貌上与这两个区都有相近之处(Young, 1993)。塔里木的早期脊椎动物化石是在最近十年才被发现并研究的，包括盔甲鱼类、棘鱼类，以及一些软骨鱼类的微体化石(刘时藩, 1993; 王俊卿等，印刷中)。就棘鱼类的面貌而言，塔里木与华南扬子区非常一致。盔甲鱼类是华南所特有的早期脊椎动物化石，其在塔里木的发现充分说明塔里木与华南同属一个早期脊椎动物区系，在中古生代时有着非常密切的联系。在过去的中国泥盆系地层区划中，宁夏中宁、中卫归属祁连山区(Chilienshan Region; Yang *et al.*, 1981; P' an, 1981)或昆仑一祁连山区(侯鸿飞等, 1988)，该区自西向东横贯塔里木、柴达木、河西走廊和中朝准地台。这一划分基本上是固定论的观点。因此，宁夏中宁、中卫(属于河西走廊)所发现的早期脊椎动物化石(潘江等, 1980, 1987)就被有些学者当作华北板块的代表(Rrtchie *et al.*, 1992; Young, 1993)，用于指示华南与华北在泥盆纪时的联系(Ritchie *et al.*, 1992, 图 36B)。实际上，河西走廊处于中国东部中朝准地台和西部昆秦褶皱系两个一级大地构造单元之间的衔接地带(潘江等, 1987)，具有与华

北板块完全不同的古生代演变历史(Li *et al.*, 1985)。因此，河西走廊与其说是华北板块的一部分，不如说是华南或扬子板块的一部分。

2. 大瓣鱼科的分布与起源中心

大瓣鱼科化石在中古生代早期脊椎动物四大区系中都有分布(图2)，延续时代从早泥盆世的Pragian期到晚泥盆世Frasnian期。相对而言，早泥盆世是大瓣鱼科的鼎盛期，共有七个属；中—晚泥盆世只有三个属，而且仅分布在欧美区。

历史生物地理学有三个主要方法或学派(Wiley, 1981)：进化生物地理学(Wallace, 1876; Matthew, 1915; Darlington, 1957)，系统发育生物地理学(Hennig, 1966; Brundin, 1966; Nelson, 1969)和隔离分化生物地理学(Croizat, 1964; Nelson, 1974; Rosen, 1978, 1979; Planick & Nelson, 1978; Nelson & Planick, 1981)。前两个学派均以起源中心的概念为基础。进化生物地理学又被称为传统的扩散学说(Patterson, 1981)，它建立在地球固定论的基础上，将扩散作为断续分布的一种主要成因动力，其主要问题是缺乏经验性的证据。在这点上，系统发育生物地理学要先进一些，它具有一个可以证明的前提假设，即边缘隔离成种模式。因此，当前的扩散学说是以系统发育生物地理学为代表的。不容否认，起源中心与扩散概念存在着方法论(或哲学)上的某些缺陷，然而，作为生物分布型式的一种成因，这两个概念仍然有效(Young, 1984)。仅仅由于它们是先验的、不可检验的，就象一些隔离分化生物地理学家那样，对自然界并不罕见的扩散现象置之不理，似乎也不妥当。边缘隔离成种模式虽然不能概括所有的成种模式，但它毕竟是其中的一种。同样，我们也并不能用隔离分化模式来解释所有的生物地理分布现象。我们认为，扩散模式与隔离分化模式是一种互补关系，它们各有侧重点，也都不完全。扩散模式可以帮助确定起源中心，而隔离分化模式更注重型式的探讨，即各土著区相互关系的判定，因此隔离分化生物地理学又被称为型式生物地理学(Young, 1984)。

关于祖先分布(ancestral distribution)，系统发育生物地理学分两种情况来估计(Patterson, 1981)。首先，假若后裔分布(descendant distribution)完全不重叠，相加即为祖先分布。其次，假若后裔分布部分重叠，重叠的部分代表祖先分布。可以看出，这里祖先分布的估计是建立在分支图的基础上。具体到大瓣鱼科，如果前面建立的分支图比较真实地反映了大瓣鱼科演化历史的话，我们可以得出下面的结论(图2)。瓣甲鱼目起源于华南，而大瓣鱼科的祖先几乎是广布的，分布区包括华南区、欧美区和东冈瓦纳区。大瓣鱼科化石在早泥盆世结束时大多绝灭，只有欧美区的一支延续到晚泥盆世Frasnian期(图3)。

3. 大瓣鱼科的隔离分化模式

隔离分化模式主要是通常建立地区分支图(area cladogram)来探讨各土著区的相互关系。该模式通过后裔分布相加来估计祖先分布。目前，在隔离分化生物地理学中，分析地区相互关系主要有两种方法。第一种是组元分析法(Component Analysis; Nelson & Platnick, 1981; Humpries & Parenti, 1986)。该方法存在一些缺陷，需要使用协和技术(consensus techniques)来分析原始资料。即使应用简约方法，所产生的组元也需要基于

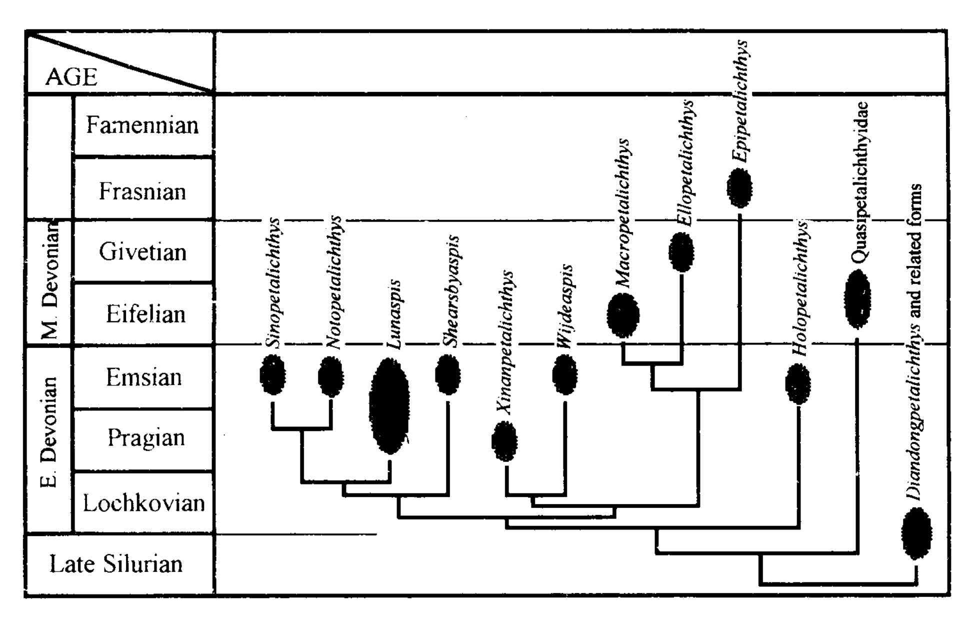


图3 瓣甲鱼类的年代地层学分布

大瓣鱼科各属之间的系统发育关系根据图2，大瓣鱼科、拟瓣鱼科和滇东瓣甲鱼之间的系统发育关系依Zhu(1991)

Fig. 3 Chrono-stratigraphic distribution of petalichthyids

The phylogenetic relationship within the Macropetalichthyidae is based on Fig. 2, and the phylogenetic relationship among the Macropetalichthyidae, Quasipetalichthyidae and *Diandongpetalichthys* is after Zhu(1991)

一些并不简约的假设去解释异常现象(Wiley, 1988)。第二种被称为布氏简约法(Brooks Parsimony Analysis; Brooks, 1981, 1985)。它通过建立地区 × 类元矩阵来获得最简约的地区分支图。这一方法克服了组元分析法的缺陷，只使用“类群分布应是最简约的”这一假设。本文尝试从大瓣鱼科的系统发育出发，使用布氏简约法来研究泥盆纪时四大脊椎动物地理区系(欧美区，东冈瓦纳区，华南区和西伯利亚区)之间的关系。

表1 大瓣鱼科十个属的地区 × 类元矩阵 B-J代表图2中的结点

Table 1 Area × taxon matrix for ten genera of the Macropetalichthyidae

Abbreviations: B-J represent the nodes in Fig. 2; EG, East Gondwana; El, *Ellopetalichthys*; Ep, *Epipetalichthys*; EU, Euramerica; Ho, *Holopetalichthys*; Lu, *Lunaspis*; Ma, *Macropetalichthys*; No, *Notopetalichthys*; SC, South China; Sh, *Shearsbyaspis*; SI, Siberia; Si, *Sinopetalichthys*; Wi, *Wijdeaspis*; Xi, *Xinanpetalichthys*

	Si	No	Lu	Sh	Wi	Xi	Ma	El	Ep	Ho	B	C	D	E	F	G	H	I	J
欧美区(EU)	0	0	1	0	1	0	1	1	1	0	1	1	1	1	0	1	1	1	1
华南区(SC)	1	0	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	0	0
东冈瓦纳区(EG)	0	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0
西伯利亚区(SI)	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0

作为分析的第一步，我们根据前面获得的大瓣鱼科的分支图(图2)以及这些大瓣鱼类的分布，建立地区 × 类元矩阵(表1)。经过计算，得到一个最简约法的地区分支图(图4)。该图表明，在泥盆纪期间，华南区与东冈瓦纳区有较密切的联系。这一结论与其它门类(如胴甲鱼类，腕足类等)历史生物地理学研究所得出的结果(Young, 1987, 1988; Ritchie *et al.*, 1992)是吻合的。此外，根据该地区分支图，我们预测在华南泥盆系地层中能够发现 *Wijdeaspis*。

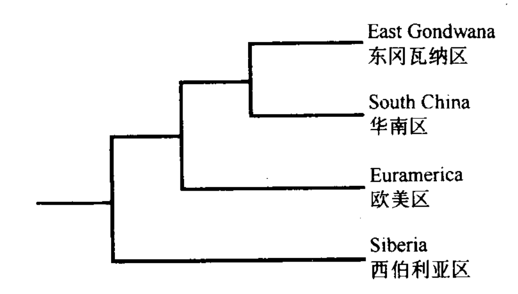


图4 根据表1数据所获得的最简约的地区分支图

Fig.4 Most parsimonious area-cladogram based on the data in Table 1

五、结 语

1. 本文描述了早泥盆世大瓣鱼科一新属新种——龙华全瓣鱼(*Holopetalichthys longhuaensis* gen. et sp. nov.)。

2. 分支系统学研究表明全瓣鱼是最原始的大瓣鱼类，它与其余的大瓣鱼类构成姊妹群。

3. 根据历史动物地理学研究，瓣甲鱼目起源于华南，而大瓣鱼科的祖先几乎是广布的，分布区包括华南区、欧美区和东冈瓦纳区。

4. 对大瓣鱼科十个现有属进行了隔离分化生物地理学分析，结果显示，在泥盆纪期间，华南区与东冈瓦纳区有较密切的联系。

致谢 张弥曼院士审阅文稿，并提出宝贵意见。张杰先生摄制图版。作者在此表示感谢。

参 考 文 献

王士涛，曹仁关，1988. 滇西早泥盆世大瓣鱼科(Macropetalichthyidae)化石的发现. 古脊椎动物学报，**26**(1):73—75

王俊卿，王念忠，朱敏(印刷中). 新疆塔里木盆地西北缘中古生代脊椎动物化石及相关地层. 塔里木石油地质研究新进展. 北京：科学出版社

方润森，江能人，范健才等，1985. 云南曲靖地区中志留世—早泥盆世地层与古生物. 昆明：云南人民出版社

刘玉海，1973，川滇泥盆纪的多鳃鱼和大瓣鱼化石. 古脊椎动物与古人类，**11**(2): 132—143

刘玉海，1975. 川滇早泥盆世无颌类. 古脊椎动物与古人类，**13**(4)：215—223

刘玉海，1979. 滇东早泥盆世北极鱼化石. 古脊椎动物与古人类，**17**(1)：23—34

刘时藩，1981. 月甲鱼化石在我国的发现. 科学通报，**26**(9)：744

刘时藩，1993. 中华棘鱼(*Sinacanthus*)化石的古地理意义. 科学通报，**38**(21)：1977—1978

朱敏，1992. 记真盔甲鱼类两新属——兼论真盔甲鱼类系统发育关系. 古脊椎动物学报，**30**(3)：169—184

朱敏，王俊卿，范俊航，1994. 云南曲靖桂家屯组与徐家冲组早期脊椎动物化石及相关生物地层问题. 古脊椎动物学报，**32**(1)：1—20

侯鸿飞，王士涛等，1988. 中国地层(7). 中国的泥盆系. 北京：地质出版社，348

潘江，王士涛，1978. 中国南方泥盆纪无颌类及鱼类化石. 华南泥盆系会议论文集. 北京：地质出版社，298—333

潘江，王士涛，1981. 云南早泥盆世多鳃鱼类的新发现. 古脊椎动物与古人类，**19**(2)：113—121

潘江，王士涛，刘时雨等，1980. 宁夏中宁泥盆纪沟鳞鱼及桨鳞鱼的发现及其意义. 地质学报，**54**：176—185

潘江，王士涛，刘运鹏，1975. 中国南方早泥盆世无颌类及鱼类化石. 地层古生物论文集，第一辑. 北京：地质出版社，135—169

潘江，霍福臣，曹景轩等，1987. 宁夏陆相泥盆系及其生物群. 北京：地质出版社

Broili F, 1929. Acanthaspiden aus dem rheinischen Unterdevon. *Sber. bayer. Ak. Wiss., math.-naturwiss. Abt., München* 1929(2): 143—163

Brooks D R, 1981. Hennig' s parasitological method: a proposed solution. *Syst. Zool.*, 30: 229—249

Brooks D R, 1985. Historical ecology: a new approach to studying the evolution of ecological associations. *Ann. Missouri Bot. Gard.*, 72: 660—680

Brundin L, 1966. Transantarctic relationships and their significance as evidenced by midges. *K. svenska Vetensk Akad. Handl.*, Ser. 4, **11**: 1—472

Croizat L, 1964. Space, time, and the form, the biological synthesis. Caracas: Published by the author

Darlington P J Jr, 1957. Zoogeography: The geographical distribution of animals. New York: Wiley

Denison R H, 1978. Placodermi. In: Schultze H P ed. Handbook of Paleoichthyology, vol. 2. Stuttgart: Gustav Fischer Verlag

Gross W, 1961. *Lunaspis broilii* und *Lunaspis heroldi* aus dem Hunsrückschiefer (Unterdevon, Rheinland). *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden*, **89**: 17—43

Hennig, W, 1966. Phylogenetic systematics. Urbana: University of Illinois Press

Humpries C J, Parenti L, 1986. Cladistic biogeography. Oxford Monographs on Biogeography. Oxford: Clarendon Press

Li Y, McWilliams M, Zhu H *et al.*, 1985. Paleozoic paleomagnetic results from the Hexizoulang Terrane, China. *Trans. Amer. Geophys. Uni. EOS*, **66**: 864

Liu Y H, 1991. On a new petalichthyid, *Eurycaraspis incilis* gen. et sp. nov., (Placodermi, Pisces) from the Middle Devonian of Zhanyi, Yunnan. In: Chang M M, Liu Y H, Zhang G R eds. Early Vertebrates and Related Problems of Evolutionary Biology. Beijing: Science Press, 139—178

Malinovskaya S P, 1973. *Stegolepis* (Antiarchi, Placodermi), a new Middle Devonian genus from Central Kazakhstan. *Paleontol. J.*, **7**: 189—199

Malinovskaya S P, 1989. Devonian Bothriolepidae (Placodermi) of Central Kazakhstan. *Ispitatelei otd Geologie*, **63**: 56—70

Mattew W D, 1915. Climate and evolution. *Ann. New York Acad. Sci.*, **24**: 171—318

Nelson G, 1969. The problem of historical biogeography. *Syst. Zool.*, **18**: 243—246

Nelson G, 1975. Historical biogeography: an alternative formalization. *Syst. Zool.*, **23**: 555—558

Nelson G, Platnick N I, 1981. Systematics and biogeography: cladistics and vicariance. New York: Columbia University Press

Norwood J G, Owen D D, 1846. Description of a new fossil fish, from the Palaeozoic rocks of Indiana. *Am. J. Sci.*, **51**: 367—371

Ørvig T, 1957. Notes on some Paleozoic lower vertebrates from Spitzbergen and North America. *Norsk. geol. Tidsskr.*, **37**: 285—353

P an K, 1981. Devonian antiarch biostratigraphy of China. *Geol Mag.*, **118**: 69—75

Patterson C, 1981. Methods of paleobiogeography. In: Nelson C, Rosen D E eds. Vicariance biogeography, a critique. New York: Columbia University Press, 446—489

Platnick N I, Nelson G, 1978. A method of analysis for historical biogeography. *Syst. Zool.*, **27**: 1—16

Ritchie A, Wang S T, Young G C *et al.*, 1992. The Sinolepidae, a family of antiarchs (placoderm fishes) from the Devonian of South China and Eastern Australia. *Records of Australian Museum*, **44**: 319—370

Rosen D E, 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.*, **27**: 159—188

Rosen D E, 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative

geography. *Bull. Am. Mus. Nat. Hist.*, **162**: 267—376

Stensiö E A. 1925. On the head of the macropetalichthyids with certain remarks on the head of the other arthrodires. *Publs Field. Mus. nat Hist.* (*Geol.*), **4**: 87— 197

Wallace A R. 1876. The Geographical distribution of animals, vols. 1–2. London: Macmillan; New York: Harper; reprint. New York & London: Hafner, 1962

Wiley E O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. New York: Wiley–Intersciences

Wiley E O. 1988. Parsimony analysis and vicariance biogeography. *Syst. Zool.* **37**: 271—290

Woodward A S. 1941. The head shield of a new macropetalichthyid(*Notopetalichthys hillsi*, gen. et sp. nov.) from the Middle Devonian of Australia. *Ann. Mag. nat. Hist.*, **8**(11): 91—96

Yang S P, P'an K. Hou H F. 1981. The Devonian System in China. *Geol. Mag.*, **118**: 113—224

Young G C, 1978. A new Early Devonian petalichthyid fish from the Taemas /Wee Jasper region of New South Wales. *Alcheringa*, **2**: 103—116

Young G C, 1981. Biogeography of Devonian vertebrates. *Alcheringa*, **5**: 225—243

Young G C, 1984. Comments on the phylogeny and biogeography of antiarchs (Devonian placoderm fishes) , and the use of fossils in Biogeography. *Proc. Linn, Soc. N. S. W.*, **107**: 443—473

Young G C, 1985. Further petalichthyid remains (placoderm fishes, Early Devonian) from the Taemas Wee Jasper region, New South Wales. *BMR J. Aust. Geol. Geophys.*, **9**: 121—131

Young G C, 1986. Cladistic methods in Paleozoic continental reconstruction. *J. Geol.*, **94**: 523—537

Young G C. 1987. Relationships between northern and southern vertebrate faunas during the Middle Palaeozoic. In: McKenzie K G ed. Shallow Tethys 2. Boston: Balkema, Rotterdam, 79—85

Young G C. 1988. Antiarchs (placoderm fishes) from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Palaeontogr.*, A202 : 1 —125

Young G C. 1990. Devonian vertebrate distribution patterns, and cladistic analysis of palaeontographic hypotheses. In: McKerrow W S, Scotese C R eds. Palaeozoic biogeography and palaeogeography. *Geol. Soc. Lond. Mem.*, **12**: 243—255

Young G C. 1993. Vertebrate faunal provinces in the Middle Palaeozoic. In: Long J A ed. Palaeozoic vertebrate biostratigraphy and biogeography. London: Belhaven Press, 293—323

Zhu M, 1991. New information on *Diandongpetalichthys* (Placodermi: Petalichthyida). In: Chang M M, Liu Y H, Zhang G R eds. Early Vertebrates and Related Problems of Evolutionary Biology. Beijing: Science Press, 179—194

Zhu M (in press). The phylogeny of the Antiarcha (Placodermi, Pisces), with the description of Early Devonian antiarchs from Qujing, Yunnan, China. *Bull. Mus. Nat. Hist. Nat.*

A NEW MACROPETALICHTHYID FROM CHINA, WITH SPECIAL REFERENCE TO THE HISTORICAL ZOOGEOGRAPHY OF THE MACROPETALICHTHYIDAE (PLACODERMI)

ZHU Min WANG Junqing

(*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044)

Key words Qujing (Yunnan), Early Devonian, Macropetalichthyidae, Historical Zoogeography

Summary

It has been recognized that South China is one of important distribution areas of the Macropetalichthyidae. Since close relatives of the Macropetalichthyidae were exclusively discovered in the Middle Paleozoic strata of South China and Ningxia, the study of early macropetalichthyids from China is key to the research on the origin and evolution of the Macropetalichthyidae. In the present paper, a new genus and species of the Macropetalichthyidae, *Holopetalichthys longhuaensis*, is described from the Early Devonian of Longhua Hill, Qujing, Yunnan. The fish-bearing bed lies in the top of the Xujiachong Formation, overlain by the Chuandong Formation. Zhu *et al.*(1994) suggested that the age of the Xujiachong Formation was Late Pragian to Early Emsian.

Subclass Placodermi M'Coy, 1848

Order Petalichthyida Jaekel, 1911

Family Macropetalichthyidae Eastman, 1898

Genus *Holopetalichthys* gen. nov.

Type species *Holopetalichthys longhuaensis* gen. et sp. nov.

Diagnosis Small-sized macropetalichthyid. Rostral and pineal plates in contact, completely separating the preorbital plates. Posterior pit-lines extending posteriorly to the mid-line, and ossification center of the nuchal plate situated at the posterior half of the plate. Supraorbital sensory canal not converging with the posterior pit-lines.

Etymology *Holo*-(Gr.) whole, entire, complete; -*petalichthys*(Gr.), often used in the generic names of the Petalichthyida. *Holopetalichthys* implies that the taxon of interest is a typical macropetalichthyid, contrary to the Quasipetalichthyidae and *Diandongpetalichthys*.

Holopetalichthys longhuaensis sp. nov.

(Fig. 1; Pl. Ⅰ)

Diagnosis As in the genus.

Holotype A complete skull-roof (IVPP cat. no. V9765).

Etymology Named after "Longhua Hill", the fossil locality.

Locality and horizon Longhua Hill, Qujing, Yunnan; Top of the Xujiachong Formation, Early Emsian.

Description The skull-roof is somewhat distorted. Part of the left side twists downwards, and is visible only in lateral view (pl. Ⅰ, 1). In addition, the dermal bones are eroded to some extent. However, some structures of the visceral side of the exoskeleton, such as the pineal pit and sensory canal system, can be detected by this kind of erosion.

The length of the skull-roof is 3.7cm in mid-line, and its maximum width is 2.9cm. The ratio between the length and width is about 1.28. Among available macropetalichthyids, the longest skull-roof exceeds 25cm in length, such as *Macropetalichthys rapheidolabis* (Denison, 1978). The small forms like *Ellopetalichthys* (Ørvig, 1957) and *Shearsbyaspis* (Young, 1985) are about 5cm in length. Thus, *Holopetalichthys* is the smallest macropetalichthyid so far known, near to *Diandongpetalichthys* (Zhu, 1991) in size.

As regard to the overall shape of the skull-roof, *Holopetalichthys* is suggestive of *Shearsbyaspis* (Young, 1985), *Lunaspis* (Gross, 1961) and *Notopetalichthys* (Ørvig, 1957). The anterior margin of the skull-roof is convex. The lateral margin has a shallow embayment, which is anterolateral to the orbital opening. The skull-roof gets its maximum width at the level of the anterior corner of obstantic margin, which faces posterolaterally. In contrast to the convex posterior margin of the skull-roof in *Lunaspis*, that in *Holopetalichthys* is more or less concave. The posterior margin of the skull-roof in *Shearsbyaspis* and *Notopetalichthys* is not preserved.

The orbital opening is well preserved, and completely enclosed by the skull-roof. The orbital opening is relatively large, about 6mm in length which is about 16% of the total length of the skull-roof. The internal mould of the pineal pit is visible between the orbital openings. The pineal pit is fairly large, and its position relatively to the orbital opening is same as *Shearsbyaspis* and *Lunaspis* among the Macropetalichthyidae. Along the mid-line, the skull-roof extends more or less downwards in front of the pineal opening. There is a very narrow, inverse V-shaped depression in the hindmost part of the skull-roof. Moreover, the skull-roof has a small depression closely in front of the orbital opening. The similar depression was suggested to exist commonly in the Macropetalichthyidae, such as *Shearsbyaspis* (Young, 1985).

Most of sutures between the skull bones are unclear, and only the rostral and pineal

bones can be delimited. The other bones are restored based on the pattern of the sensory canal system. The rostral and pineal plates are in contact, and completely separate the preorbital plates. Among the Macropetalichthyidae, this kind of relationship between the rostral and pineal plates is also found in *Shearsbyaspis*. The rostral plate is relatively short, and its anterior margin is convex. The pineal plate is rectangular in shape, and has a pineal pit on its visceral side. Behind the pineal plate, the plate forming the middle row of the skull-roof should be the nuchal plate, which is very long. The ornamentation of the skull-roof is composed of discrete tubercles.

The sensory canal system in *Holopetalichthys* is of typical petalichthyid pattern (Zhu, 1991). Among petalichthyids, the supraorbital canals and posterior pit-lines extends to the ossification center of the nuchal plate. They either converge together, as in *Macropetalichthys* and *Sinopetalichthys*, or still separate from each other, as in *Lunaspis*. The posterior pit-lines proceed posteriorly to the mid-line, and the ossification center of the nuchal plate lies in the posterior half of the plate. This makes a remarkable contrast with the other macropetalichthyids, in which the posterior pit-lines proceed horizontally or anteriorly to the mid-line, and the ossification center of the nuchal plate lies in the anterior half of the plate. In addition, the supraorbital canals and posterior pit-lines of the new species do not converge together, similar to *Lunaspis*.

Remarks *Holopetalichthys* can be assigned to the Petalichthyida by its sensory canal system of the skull-roof. It differs from *Quasipetalichthys*, *Eurycaraspis*, *Diandongpetalichthys* and *Neopetalichthys* by its dorsally situated orbital openings, which is one of the most important synapomorphies of the Macropetalichthyidae. Among the Macropetalichthyidae, *Holopetalichthys* is most suggestive of *Shearsbyaspis* (Young, 1985). They are neither like *Macropetalichthys*, *Xinanpetalichthys* and *Wijdeaspis*, which have fused rostropineal plate, nor like *Lunaspis*, *Notopetalichthys* and *Sinopetalichthys*, which have the rostral and pineal plates separated by the preorbital plates. By outgroup comparison, the similarity between *Holopetalichthys* and *Shearsbyaspis* (rostral and pineal plates in contact, separating preorbital plates) is symplesiomorphy of the Macropetalichthyidae. This character is also found in the Quasipetalichthyidae (Liu, 1991). *Shearsbyaspis* differs from *Holopetalichthys* by its ornamentation with low concentric or radiating ridges, and the path of posterior pit-lines. In *Shearsbyaspis*, the posterior pit-lines proceed anteriorly to the mid-line, and the ossification center of the nuchal plate lies in the anterior half of the plate, whereas in *Holopetalichthys* the posterior pit-lines extend posteriorly to the mid-line, and the ossification center of the nuchal plate lies in the posterior half of the plate.

Discussion

1. Preliminary study of the phylogenetic position of *Holopetalichthys*

In the present paper, the cladogram of the Macropetalichthyidae is proposed. That

the skull-roof encloses the orbital openings is the most important synapomorphy of the Macropetalichthyidae (Zhu, 1991). Another possible synapomorphy is the preorbital recess of the skull-roof, which is found in *Shearsbyaspis*, *Lunaspis*, *Wijdeaspis* (Young, 1985) and *Holopetalichthys*. In the character analysis, the Quasipetalichthyidae and *Diandongpetalichthys* are used as the outgroups to determine the polarity of character. In *Holopetalichthys*, the posterior pit-lines extend posteriorly to the mid-line, and the ossification center of the nuchal plate lies in the posterior half of the plate. This feature is also found in a group of petalichthyids, represented by *Diandongpetalichthys*, whose growth-series study indicates that the posterior pit-line extending posteriorly to the mid-line is plesiomorphic. In *Holopetalichthys*, the rostral and pineal plates are in contact, and completely separate the preorbital plates. By outgroup comparison, this character is also plesiomorphic to the Macropetalichthyidae. Therefore, we consider that *Holopetalichthys* is the most primitive macropetalichthyid, and forms the sister group of the other macropetalichthyids. In the latter, the posterior pit-lines proceed horizontally or anteriorly to the mid-line, and the ossification center of the nuchal plate lies in the anterior half of the plate.

Two evolutionary branches can be identified among the macropetalichthyids except *Holopetalichthys*. The first branch is represented by *Shearsbyaspis* and *Lunaspis*, whose dermal bone is ornamented with low concentric or radiating ridges. In this branch, the exception is *Notopetalichthys* which is deficient of this kind of ornamentation. However, it is most suggestive of *Sinopetalichthys* by other synapomorphies, such as the rostral and pineal plates separated by the preorbital plates, the orbital opening relatively far from the lateral margin of the skull-roof. On the basis of the principle of parsimony, *Notopetalichthys* is regarded as the sister group of *Sinopetalichthys*. Another branch is exemplified by *Macropetalichthys* and *Wijdeaspis*, whose rostral and pineal plates are fused into a rostro-pineal plate.

2. Early Vertebrate Faunal Provinces in the Middle Paleozoic

Five vertebrate faunal provinces (South China, East Gondwana, Euramerica, Siberia, and Tuva) were proposed by Young (1981) based on the Devonian Early Vertebrates. Tuva is a small province, and shown as part of Siberia block on most Devonian reconstruction (Young, 1990, 1993). Therefore, while we discuss the biogeography of Early Vertebrates in the Middle Paleozoic, the elementary problem is the interrelationship among the former four provinces.

During the Middle Paleozoic, apart from these five provinces, other paleogeographic units bearing Early Vertebrates include Kazakhstan, West Gondwana and Tarim. There are some units, such as Turkey, Iran, Arabia, Shan-Thai Terrain (including West Yunnan of China) attaching on the north margin of the Gondwana Continent during this period. Kazakhstan yields mainly antiarchs with respect to Early Vertebrates. Its endemic genera, such as *Tenizolepis* and *Stegolepis* (Malinovskaya, 1973, 1989), have close affinity to *Hunanolepis* and *Jiangxilepis* of South China (Young, 1993; Zhu, in press), indicating the

connection between these two provinces. West Gondwana lies between Euramerica and East Gondwana, and has both Euramerica and East Gondwana aspects (Young, 1993). During the past decade, many Early Vertebrate fossils including acanthodians, galeaspids and chondrichthyans were found in Tarim, China. As to the aspect of acanthodians, Tarim is very consistent with South China, especially Lower Yangtze. Galeaspids are endemic to South China Province. Their discoveries in Tarim indicate that Tarim and South China belong to the same Early Vertebrate Province. The Devonian Early Vertebrates in North China are doubtful. The Early Vertebrate fossils from Ningxia and Gansu of China (Hexizoulang Terrane) have been considered by some authors as the representatives of Early Vertebrates in North China, and used as evidence of the connection between South China and North China during Middle Devonian (Ritchie *et al.*, 1993; Young, 1993). In fact, Hexizoulang Terrane is situated between the Sino – Korean Platform (North China block) and Kunlunshan – Qinling Geosyncline, and has separate geological history to North China. Thus, we would rather considered Hexizoulang Terrane as part of South China rather than as part of North China.

3. Hennigian dispersal analysis of the Macropetalichthyidae

The Macropetalichthyidae distributed in Euramerica, Siberia, East Gondwana and South China, four large Early Vertebrate Provinces during the Middle Paleozoic. Based on the Hennigian dispersal analysis (Patterson, 1981), we can have following conclusions. The Petalichthyida originated in South China. The ancestor of the Macropetalichthyidae is almost cosmopolitan, and is distributed in South China, Euramerica and East Gondwana. Most of the Macropetalichthyidae had become extinct by the end of Early Devonian, and only one branch lasted to the Frasnian in Euramerica.

4. Vicariance analysis of the Macropetalichthyidae

In our view, the Hennigian dispersal analysis and variance analysis complement each other. Each of them has its emphasis. The dispersal analysis is helpful to determine the origin center of the group, whereas the vicariance analysis lies stress on the distribution pattern, i. e., the relationship among endemic areas. In the present study, the area × taxon matrix of the Macropetalichthyidae (Table 1) is first constructed after the cladogram of the group and their distributions. Then, Brooks Parsimony analysis is used to obtain the most parsimonious area cladogram (Fig.4). This area cladogram reflects that South China and East Gondwana had close connection during the Devonian. This result is consistent with the conclusions from paleobiogeographic studies of other groups (*e. g.* antiarchs, brachiopods; Young, 1987, 1988; Ritchie *et al.*, 1992).

图版 I 说明(Explanations of plate I)

龙华全瓣鱼(新属、新种) *Holopetalichthys longhuaensis* gen. et sp. nov. V 9765, 正型标本(Holotype), ×3.3

1. 颅顶甲侧视(lateral view of skull – roof); 2. 颅顶甲背视(dorsal view of skull – roof)



1



2